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Living in groups: spatial-moment dynamics with neighbour-biased movements

Rachelle N. Binny^{1,2}, Richard Law³, Michael J. Plank^{2,4,*}

1. Manaaki Whenua Landcare Research, Lincoln 7640, New Zealand.

2. Te Pūnaha Matatini, New Zealand.

3. Department of Biology, University of York, York YO10 5DD, United Kingdom.

4. School of Mathematics and Statistics, University of Canterbury, Christchurch 8140, New Zealand.

* Corresponding author email: michael.plank@canterbury.ac.nz

Abstract

Herd formation in animal populations, for example to escape a predator or coordinate feeding, is a widespread phenomenon. Understanding which interactions between individual animals are important for generating such emergent self-organisation has been a key focus of ecological and mathematical research. Here we show the relationship between the algorithmic rules of herd-forming agents, and the mathematical structure of the corresponding spatial-moment dynamics. This entails scaling up from the rules of individual, herd-generating behaviour to the macroscopic dynamics of herd structure. The model employs a mechanism for neighbour-dependent, directionally-biased movement to explore how individual interactions generate aggregation and repulsion in groups of animals. Our results show that a combination of mutually attractive and repulsive interactions with different spatial scales is sufficient to lead to the stable formation of groups with a characteristic size.

Keywords: collective behaviour; herd formation; moment closure approximation; neighbourhood interactions; spatial point process.

1 Introduction

The self-organisation of animals into herds, and the use of individual-based models to learn about the rules underlying this process, is a core subject in behavioural ecology (Krause et al., 2002). Herd formation is most often considered in terms of movements of individuals, biased by their interactions at small spatial scales. However, these movements can affect the dynamics of populations and communities at larger spatial scales. In his seminal work, “Geometry for the selfish herd”, Hamilton (1971) proposed that aggregation of animals into groups or herds, could be driven by the ‘selfish’ desire of an animal to reduce its predation risk by manoeuvring to positions that would place other population members closer to the predator. Underlying this idea was the concept of an animal’s *domain of danger*, a region of space containing all points nearer to that individual than to any other individual. The larger an animal’s domain of danger, the greater its risk of predation, and Hamilton therefore theorised that aggregation arose simply due to each animal undergoing movements towards its nearest neighbour, to reduce the size of its domain of danger. Stemming from this original idea, James et al. (2004) considered a model with greater biological realism, by incorporating a *limited domain of danger*, representing either a limited detection range or attack range of predators, that could be applied to animal groups of finite size. Further work by Reluga and Viscido (2005) pointed out that rules for generating realistic selfish herds need interactions beyond an individual’s nearest neighbours, and showed how predation-based selection could increase the influence of distant neighbours. Other models explored animal aggregation behaviour by introducing sensory zones of individuals, for example zones of repulsion or attraction that drive animals towards or away from neighbouring individuals, giving rise to higher order structure in the population (Couzin et al., 2002; Wood and Ackland, 2007; Bode, 2011; Herbert-Read et al., 2011). One such model, proposed by Lukeman et al. (2010), used imagery data to infer individual zones of repulsion-alignment-attraction to describe self-aggregation in surf scoter flocks.

In addition to individual-based models, other common modelling approaches for herd formation involve the use of mathematical equations of motion for individuals or populations. For example, “Lagrangian” equations of motion describe individuals’ trajectories in terms of forces and velocities. “Eulerian” continuum equations (i.e. partial differential equations), based on a diffusion approximation of random motion, are also widely employed to describe the evolution (in time and space) of mean-field density for swarms (Parrish and Edelstein-Keshet, 1999). The key problem with mean-field models is that they consider only the first spatial moment (the average density of individuals) and invoke an assumption that all in-

70 individuals interact in proportion to this average density (i.e. equivalent to
71 assuming a well-mixed population or that all interactions are long-ranged),
72 thereby ignoring any spatial structure in a population. This can give mis-
73 leading results for systems where spatial structure is an important driver
74 of the population dynamics (Law et al., 2003).

75 Models for the dynamics of spatial moments deal explicitly with local
76 spatial structure, and avoid the limitations of mean-field models by us-
77 ing higher-order spatial moments. The second spatial moment, i.e. the
78 density of pairs of individuals as a function of their spatial separation,
79 carries information on local spatial structure, and there is now a substan-
80 tial body of theory for spatial-moment dynamics up to second order for
81 birth-death-movement processes (Bolker and Pacala, 1997; Dieckmann and
82 Law, 2000; Murrell and Law, 2003). This theory has been extended to
83 consider multiple interacting species (Plank and Law, 2015), for example
84 in predator-prey systems (Murrell, 2005; Barraquand and Murrell, 2013).
85 A formal mathematical derivation that allows construction of a dynami-
86 cal system for the second spatial moment in the presence of directionally-
87 biased movement has been given by (Middleton et al., 2014; Binny et al.,
88 2015, 2016a) and extended to include birth and death processes (Binny
89 et al., 2016b). This mechanism for neighbour-dependent directional bias
90 has been shown to be a strong driver of spatial structure, such as aggre-
91 gation, in motile cell populations (Binny, 2016). The directionally-biased
92 movement modelling framework has been extended to multiple species by
93 Surendran et al. (2018b) in the context of cell-obstacle interactions and by
94 Surendran et al. (2018a) to chase-escape dynamics. However, directional
95 movement of animals, as they respond to cues from their neighbourhoods,
96 have not previously been part of this framework (but see Murrell and Law
97 (2000) for nondirectional, environment-dependent movement).

98 Spatial moment dynamics are capable of providing mechanistic under-
99 standing of the effects of individual interactions that repeated simulations
100 of individual-based models alone cannot. Although it is not typically pos-
101 sible to obtain closed-form solutions for the spatial moments, which must
102 be approximated numerically, the structure of the equations can provide
103 analytical insights into the relationships between model parameters and
104 solutions. For example, spatial moment approximations have revealed:
105 how and why spatial structure affects population carrying capacity (Law
106 et al., 2003); new mechanisms for coexistence (Murrell and Law, 2003); the
107 relative importance of different drivers of spatial structure (Binny et al.,
108 2016b); and an analytical equivalence between mean population density
109 and interaction range (Binny, 2016). Although straightforward to simu-
110 late in principle, individual-based models are stochastic processes with a
111 very high dimensional state space and are not amenable to analytical ap-

112 proaches except in special cases (Blath et al., 2007). In addition, although
 113 individual-based models are relatively efficient to simulate for small pop-
 114 ulations, the computational cost for models with interactions among in-
 115 dividuals increases faster than linearly with population size (Binny et al.,
 116 2016b). In contrast, the computational cost of solving a spatial moment
 117 dynamics approximation is insensitive to population size (Surendran et al.,
 118 2018b) so this represents an efficient alternative to individual-based models
 119 for large or growing populations.

120 The purpose of this paper is two-fold. First, we employ new mathemati-
 121 cal theory recently developed in the context of collective cell behaviour, that
 122 allows scaling up from directionally-biased agent movements to macroscopic
 123 dynamics (Binny et al., 2016a; Surendran et al., 2018b), and demonstrate
 124 how it can be applied in the ecological setting of herd formation in animals.
 125 The key mathematical expressions encoded in the rules of the individual-
 126 based model become clear in doing this. Secondly, we show that the spatial
 127 properties of herd formation are captured by the macroscopic dynamics,
 128 through appropriate choice of interaction kernels for directionally-biased
 129 movement. **This provides a foundation to bring biased movement**
 130 **into the earlier models of spatial-moment dynamics that focus on**
 131 **births, deaths and unbiased movement (Plank and Law, 2015).**
 132 **The framework will enable herd development to be studied in**
 133 **the broader context of population and community dynamics. To**
 134 **facilitate this future work, the mathematical derivations are given**
 135 **in a multi-species setting.**

136 2 Stochastic, individual-based model

137 Spatial-moment dynamics of birth, death and growth processes have been
 138 dealt with previously (Bolker and Pacala, 1997; Dieckmann and Law, 2000;
 139 Murrell and Law, 2003; Adams et al., 2013). Therefore here we con-
 140 sider only movement of individuals of fixed types. We first consider an
 141 individual-based model for motile agents. For generality, we allow individ-
 142 uals to be of an arbitrary number of types, indexed $i \in \{1, \dots, i_{\max}\}$. These
 143 could be species allowing, for instance, spatial interactions of predators and
 144 herd-living prey (the indexing can be ignored if all individuals are of the
 145 same type). Processes take place in a continuous two-dimensional space,
 146 which is large compared with the scale over which individuals interact and
 147 move; a point in the space is given by the vector $x = (x_1, x_2)$ of Cartesian
 148 coordinates.

149 2.1 Model for biased movement

150 The population comprises a fixed number n of individuals numbered $p =$
 151 $1, \dots, n$, and the state at time t is characterised by their types and locations
 152 (i_p, x_p) . Individual p moves in a series of discrete steps, which occur at a
 153 rate M_p that may depend on its neighbourhood. This is a Poisson process
 154 over time, so the probability of movement in a short period δt is $M_p \delta t +$
 155 $O(\delta t^2)$. Movement events are assumed to occur as instantaneous jumps
 156 (i.e. a position jump process). As soon as a movement takes place, the
 157 state of the system is changed, potentially leading to a change in M_p as
 158 well.

159 We allow both an intrinsic and a neighbourhood contribution to the
 160 movement rate, given by

$$161 \quad M_p = m_{i_p} + \sum_{q \neq p} w_{i_p i_q}(x_p, x_q). \quad (1)$$

162 Here m_i is the intrinsic component of the movement rate for type i , and
 163 $w_{i_p i_q}(x_p, x_q)$ is an extra contribution to the movement rate caused by a
 164 neighbouring individual q of type i_q at location x_q . The contribution may
 165 depend on the location and type of both p and q . The weight typically
 166 attenuates with distance from p to q and could depend on whether individ-
 167 ual q is the same species or, say, a predator species. The overall effect of
 168 neighbours is obtained by summing over all q , excluding individual p itself.

169 When individual p moves from x_p , it jumps to another location $u_p =$
 170 $x_p + \xi$ where ξ is a random variable in \mathbb{R}^2 with a bivariate probability
 171 density function (PDF) of the form

$$172 \quad \hat{\mu}_p(\xi) = f_{i_p}(|\xi|) \hat{g}_p(\arg(\xi)), \quad (2)$$

173 where $\arg(\xi) \in [0, 2\pi)$ denotes the direction of the vector ξ . The PDF in
 174 Eq. (2) is separated into two independent parts for the distance moved $|\xi|$
 175 and the direction of movement $\arg(\xi)$. For simplicity, we assume that $f_i(|\xi|)$
 176 is neighbourhood-independent (though it may depend on the individual's
 177 type i) and given by the Gaussian function with mode r_i and variance s_i^2 :

$$178 \quad f_i(|\xi|) = C_i e^{-\frac{(|\xi| - r_i)^2}{2s_i^2}}, \quad 0 \leq |\xi| \leq r_{i,\max}, \quad (3)$$

179 where C_i is a normalisation constant. In contrast to the distance moved,
 180 the direction of movement does depend on the neighbourhood of individual
 181 p , and is the core mechanism underpinning herd development here. The
 182 neighbourhood dependence takes the form of a bias vector $\hat{\eta}_p$ for individual
 183 p , defined below, that provides the parameters for a circular probability
 184 distribution for the direction of movement.

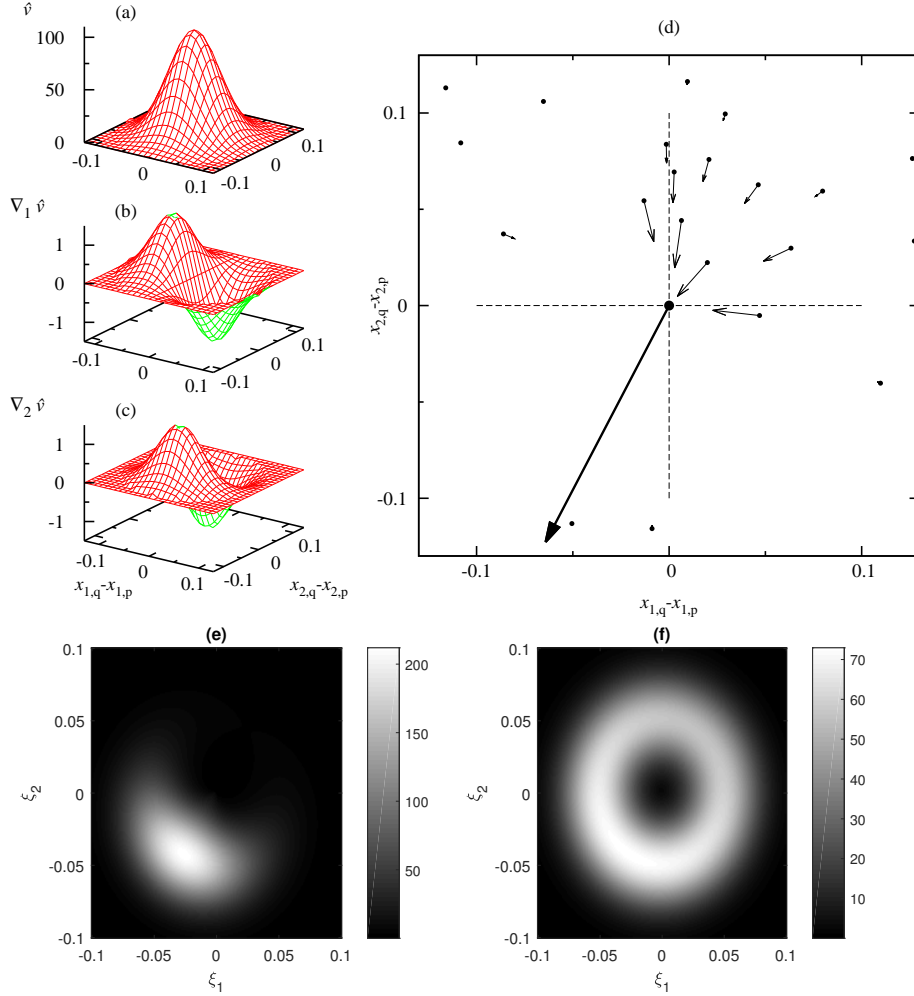


Figure 1: Schematic diagram showing how the bias vector and the movement distribution of a focal individual are constructed. (a) A bias kernel v , from which the gradient vector ∇v , whose x_1, x_2 components are plotted in (b) and (c), is obtained. (d) Contribution of neighbouring individuals (light arrows) to the bias vector of the focal individual at the origin (bold arrow). Note that the light arrows are not the bias experienced by the neighbouring individuals, but their contribution to the bias of the focal individual. The direction of the bias vector determines the preferred direction and its magnitude determines how tightly peaked the distribution is around the preferred distribution. Note the bias vector does not determine the new location of the focal individual. (e, f) Bivariate probability density function Eq. (2) for the movement vector ξ of the focal individual in the case of strong bias ($\beta = 0.15$) and weak bias ($\beta = 0.01$) respectively. Movement distance is distributed according to Eq. (3) with $r = 0.05$, $s = 0.02$, $r_{\max} = r + 3s$.

185 The bias vector is obtained from the gradient vector of a bias kernel
 186 function that carries the key biological information. As an example, we de-
 187 scribe the construction of a bias vector for a single focal individual located
 188 at the origin in Fig. 1. This starts with a bias kernel function $v_{i_p i_q}(x_q - x_p)$,
 189 here a standard Gaussian function of the distance $x_q - x_p$ between two indi-
 190 viduals (Fig. 1a), potentially dependent on both the focal individual's type
 191 i_p and the neighbouring individual's type i_q . The kernel gives a gradient
 192 vector $\nabla v_{i_p i_q}(x_q - x_p)$, i.e. the partial derivatives of $v_{i_p i_q}$ in the two spatial
 193 dimensions (Fig. 1b, c). The contribution of neighbouring individual q of
 194 type i_q and location x_q to the bias vector of the focal individual p is the gra-
 195 dient vector evaluated at $x_q - x_p$ (light arrows on neighbouring individuals
 196 in Fig. 1d). A neighbour vector that points towards the origin corresponds
 197 to a repulsive effect of the neighbour on the focal individual (an outward
 198 arrow would be an attractive effect). Summing all neighbour vectors gives
 199 the bias vector for the focal individual (bold arrow on the focal individual
 200 in Fig. 1d):

$$\hat{\eta}_p = \beta_{i_p} \sum_{q \neq p} \nabla v_{i_p i_q}(x_q - x_p), \quad (4)$$

202 where β_{i_p} is a parameter scaling the overall strength of bias. In the example
 203 (Fig. 1d), the neighbourhood gives the focal individual a preferred direction
 204 of movement away from the cluster of individuals on its upper right-hand
 205 side. Note that changing the sign of the bias kernel in Fig. 1a would reverse
 206 the direction of all arrows in Fig. 1d and hence produce an attractive rather
 207 than a repulsive bias.

208 Once the bias vector $\hat{\eta}_p$ for individual p is computed, its direction of
 209 movement θ is drawn from the von Mises distribution (independent of the
 210 distance moved) with preferred direction $\arg(\hat{\eta}_p)$ and concentration $|\hat{\eta}_p|$.
 211 This distribution has probability density function

$$\hat{g}_p(\theta) = g(\theta, \hat{\eta}_p) = \frac{\exp(|\hat{\eta}_p| \cos(\theta - \arg(\hat{\eta}_p)))}{2\pi I_0(|\hat{\eta}_p|)}, \quad (5)$$

213 where I_0 is the modified Bessel function of the first kind and zero order.
 214 If the magnitude of the bias vector is large, the von Mises distribution is
 215 tightly peaked around $\arg(\hat{\eta}_p)$, meaning the individual is highly likely to
 216 move in a direction close to the preferred direction (Fig. 1e). This situation
 217 would arise if the focal individual has multiple near neighbours exerting
 218 bias in similar directions (as in the example in Fig. 1d). Conversely, if the
 219 magnitude of the bias vector is small, the von Mises distribution is more
 220 broadly distributed (Fig. 1f). In the limit where the bias vector has zero
 221 magnitude, the von Mises distribution is a uniform distribution on $[0, 2\pi)$,
 222 meaning the focal individual is equally likely to move in any direction. This
 223 situation would arise if the focal individual has no near neighbours, or has

224 neighbours that are symmetrically positioned on opposite sides such that
 225 their contributions to the bias vector cancel one another out.

226 2.2 Implementation

227 We initialised realizations of the stochastic individual-based process with
 228 a fixed population of $n = 200$ individuals of a single type. The individuals
 229 were distributed in a unit arena as a spatial Poisson process at the start
 230 of each realization; in other words, each individual's location was chosen
 231 uniformly at random and independently of all other individuals. Distances
 232 are given relative to the unit of the arena. We used periodic boundary
 233 conditions, and updated the state of the system in continuous time using
 234 the Gillespie algorithm (Gillespie, 1977). For simplicity, we assumed the
 235 movement rate to be independent of neighbourhood by setting $w_{ipiq} = 0$
 236 for all p and q in Eq. (1), leaving in place only an effect of neighbours on
 237 the direction of intrinsic movements.

238 Eqs. (2)–(5) define the bivariate movement distribution of a focal in-
 239 dividual p . Vectors ξ from this bivariate distribution were obtained by
 240 independently generating the distance and direction of movement. The
 241 probability that the distance moved $|\xi|$ by an individual of type i lies in
 242 the infinitesimal interval $[r, r + dr]$ is $r f_i(r) dr$. Hence, movement distance
 243 of an individual of type i has PDF

$$244 \quad h_i(r) = r f_i(r).$$

245 Random numbers from this distribution were generated via the following
 246 rejection sampling algorithm:

- 247 1. Generate a normally distributed random number $R \sim N(r_i, s_i^2)$
- 248 2. If R lies outside the interval $[0, r_{i,\max}]$, go to step 1. This results in a
 249 sample from the distribution with PDF $f_i(r)$ specified by Eq. (3).
- 250 3. Accept R with probability $P(R) = R/r_{i,\max}$, otherwise go to step
 251 1. This results in a sample from the distribution with PDF $h_i(r)$ as
 252 required.

253 The direction of movement θ was generated from the von Mises distribution
 254 with PDF given by Eq. (5). This requires the bias vector $\hat{\eta}_p$ for individual
 255 p to be calculated, according to Eq. (4).

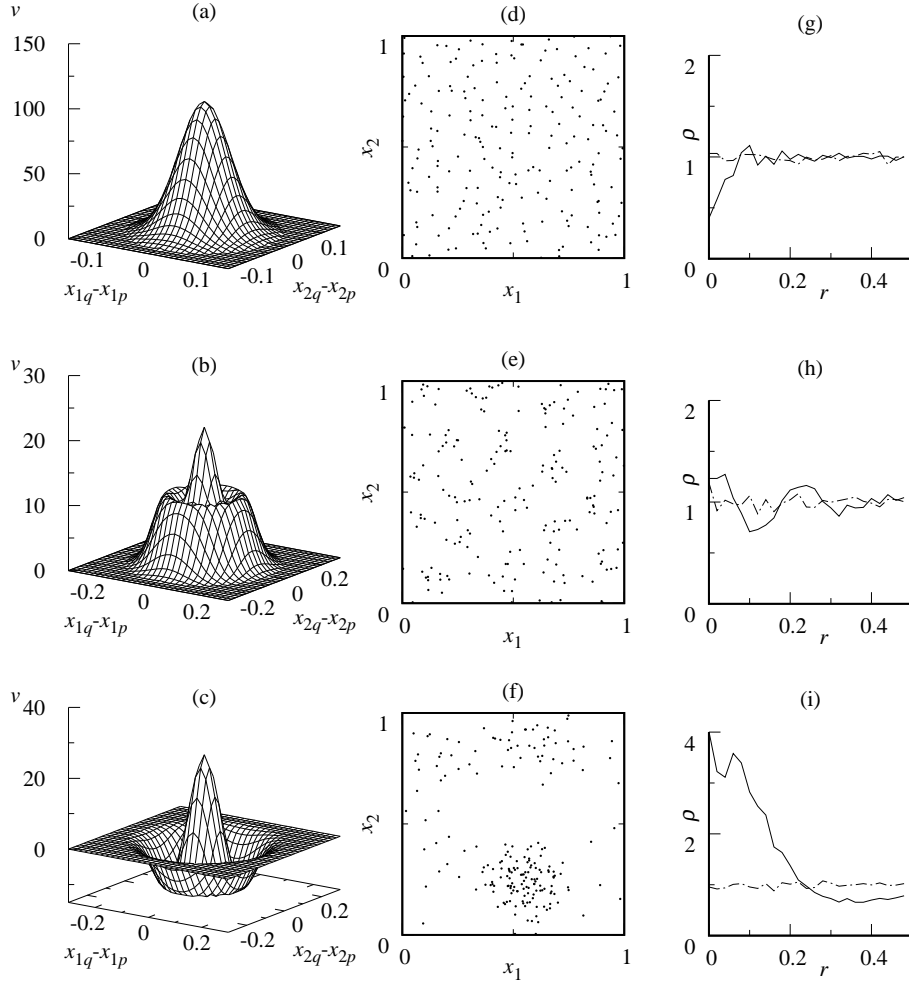


Figure 2: Territories and clusters developing from contrasting bias kernels. (a) A single positive Gaussian function Eq. (6) ($\sigma_1 = 0.04$, $N = 0.0099$) leads to formation of territories. (b) Adding a second Gaussian function, Eq. (7), that peaks at a distance $\bar{r} = 0.12$ from the origin ($\sigma_1 = \sigma_2 = 0.04$, $N = 0.0477$, $k_2 = 0.5$) leads to small clusters. (c) Subtracting a second Gaussian function, Eq. (7), that reaches its minimum at a distance $\bar{r} = 0.12$ from the origin ($\sigma_1 = \sigma_2 = 0.04$, $N = 0.0401$, $k_2 = -0.5$) leads to a single large cluster. Gaussian functions in the bias kernels were truncated at ± 3 standard deviations. Bias strength of the gradient vector $\beta = 0.01$. (d),(e),(f) Snapshots of locations of individuals at time $t = 10$; the spatial patterns change continuously over time, starting from a spatial Poisson process. (g),(h),(i) Contrasting pair correlation functions $\rho(r)$ of the spatial patterns develop by $t = 10$ (continuous lines, $\delta r = 0.02$); the dash-dot lines show $\rho(r)$ at time $t = 0$. Neighbourhoods act only on the direction of movement here, not on the rate of movement. Movement distance is distributed according to Eq. (3) with $r = 0.05$, $s = 0.02$, $r_{\max} = r + 3s$. Movement rate $m = 1$.

2.3 Biased-movement kernels and spatial structure

The choice of a kernel for biased movement is a biological matter with far-reaching consequences. Fig. 2 gives three examples. The first is a single Gaussian function centred on the origin

$$(a): v_{i_p i_q}(r) = \frac{1}{N} e^{-r^2/2\sigma_1^2} \quad (6)$$

where $r = |x_q - x_p|$ is the distance of neighbour q from focal individual p , σ_1 is a measure of the width of the function, and N is a normalisation constant. The second and third examples combine a Gaussian function centred on the origin with one offset from the origin by an amount \bar{r} and with width σ_2 :

$$v_{i_p i_q}(r) = \frac{1}{N} (e^{-r^2/2\sigma_1^2} + k_2 e^{-(r-\bar{r})^2/2\sigma_2^2}) \quad (7)$$

the weight k_2 of the outer function having different signs: (b) $k_2 > 0$, and
(c) $k_2 < 0$.

A kernel based on the single Gaussian function generates a gradient vector that points towards the origin, creating a region of repulsion around each individual. This means that individuals tend to move away from near neighbours (Fig. 2a), leading to territory formation (Fig. 2d). A kernel based on a double Gaussian function in which the outer Gaussian is positive ($k_2 > 0$, Fig. 2b), generates three concentric rings: an inner ring where the gradient vector points towards the origin, an intermediate ring where it points away from the origin, and an outer ring where it points towards the origin. This creates short-range repulsion, medium-range attraction and long-range repulsion, leading individuals to form small clusters (Fig. 2e). A kernel based on a double Gaussian function, in which the outer Gaussian is negative ($k_2 < 0$, Fig. 2c), generates two concentric rings: an inner ring where the gradient vector points towards the origin, and an outer ring where it points away from the origin. This creates short-range repulsion and long-range attraction, leading towards coalescence of the population into a single mega-herd (Fig. 2f). The reverse order (attraction-repulsion) would lead to collapse of individuals within groups to a single point, which would not be biologically reasonable.

Short-range repulsion (Fig. 2a, d) creates space around individuals, and is a natural basis for territories, defended by individuals or groups, that come about from scarcity of resources (Maher and Lott, 1995). Adding longer-range attraction (Fig. 2c, f) allows for benefits of living in groups, such as a reduced risk of predation, increased chance of detecting predators, and less need for individual vigilance (Hamilton, 1971; Pulliam, 1973; Elgar, 1989). With the short-range repulsion still in place, some space around

284 individuals remains and this can lead to remarkable spatial structure, such
 285 as that observed in king penguin colonies (Gerum et al., 2018). However,
 286 the combination of local repulsion and longer-range attraction can lead to
 287 very large groups forming (Olson et al., 2009). In practice, populations
 288 often break up into much smaller groups because of the costs of living to-
 289 gether, such as the need for synchronized behaviour (Gajamannage et al.,
 290 2017), levels of stress (Markham et al., 2015), possibly the spread of disease
 291 (Griffin and Nunn, 2012; Sah et al., 2017), and competition/cooperation
 292 between males (DuVal, 2007). Adding a further outer region of repulsion
 293 (Fig. 2b, e) allows break-ups to happen, the smaller groups being dis-
 294 tributed non-randomly over space, with spatial structure inside the groups
 295 themselves.

296 The spatial structures in Fig. 2 are clearly quite different, and this
 297 difference is summarised in their pair correlation functions (Fig. 2g,h,i). A
 298 pair correlation function $\rho_{ij}(r)$ is a standard, second-order spatial statistic,
 299 based on the density of pairs of points of type i, j as a function of the
 300 distance r between them (Illian et al., 2008). In the absence of spatial
 301 structure at a distance r , $\rho_{ij}(r)$ takes a value 1; if there is an excess of
 302 pairs (clustering), $\rho_{ij}(r) > 1$; if there is a lack of pairs (regular pattern),
 303 $\rho_{ij}(r) < 1$. Thus the space that individuals create around themselves in
 304 Fig. 2d shows up as a lack of pairs at short distance in the pair correlation
 305 in Fig. 2g. The clusters that form in Fig. 2e appear as an excess of pairs at
 306 short distances in Fig. 2h, and a lack of pairs at slightly longer distances.
 307 The clusters themselves are not distributed at random across space, and
 308 leave an attenuating oscillatory signal in the pair correlation as distance
 309 increases. The location of the secondary peak in Fig. 2h at around $r = 0.2$
 310 corresponds to the typical distance between adjacent clusters. The mega-
 311 herd developing in Fig. 2f appears as a large peak of pairs at short distances
 312 from the interaction of local repulsion and longer-distance attraction, with
 313 pairs becoming less frequent beyond the peak (Fig. 2i). The function does
 314 not tend to 1 at large distances, because the cluster is on the same spatial
 315 scale as the arena.

316 At a single point in time, repeated realizations of the stochastic processes
 317 from the same initial statistical distribution have different spatial configu-
 318 rations, but the same basic information is retained in the pair correlation
 319 functions. As time goes on, the spatial patterns change, and the pair cor-
 320 relation functions track the developing spatial structure. This tracking is
 321 evident in Fig. 2g,h,i. The realizations all started as Poisson processes lack-
 322 ing spatial structure, and with pair correlation functions close to 1 at all
 323 distances. But, by $t = 10$, the functions are quite distinct from one another,
 324 as shown in Fig. 2. The significance of the time-dependent pair correla-
 325 tion becomes important below, because a measure of this kind becomes the

state variable of the spatial-moment dynamics. In some ecological systems, statistical stationarity may eventually be reached. But in others, such as predator-prey systems, it is conceivable that the pair correlation functions could develop periodic behaviour and continue to change indefinitely. The long-term behaviour of the pair correlation function under a given choice of bias kernel is not sensitive to the particular choice of initial conditions.

3 Spatial-moment dynamics

Here we show how the algorithmic rules of the individual-based stochastic process can be described mathematically to give deterministic approximation in the form of a dynamical system for the second spatial moment.

3.1 Definition of spatial moments

In defining the spatial moments, it helps to think of small regions of area h , so that the $O(h^2)$ probability of containing more than one individual is vanishingly small. Formally, the first spatial moment at time t is the expected value of the density obtained from the stochastic process at time t , in the limit as $h \rightarrow 0$:

$$Z_{1,i}(x) = \lim_{h \rightarrow 0} \frac{E[n_i(\delta x)]}{h}, \quad (8)$$

where $n_i(\delta x)$ is the number of individuals of type i in the region δx centred on x .

In the case of the second moment, we consider two regions of area h : δx centred on x containing n_i individuals of type i , and δy centred on y containing n_j individuals of type j . The second spatial moment at time t is the expected value of the pair density from the stochastic process at time t , in the limit as $h \rightarrow 0$ (Plank and Law, 2015):

$$Z_{2,ij}(x, y) = \lim_{h \rightarrow 0} \frac{E[n_i(\delta x)n_j(\delta y) - \delta_{ij}n_i(\delta x \cap \delta y)]}{h^2}. \quad (9)$$

The second term in the numerator (with Kronecker delta δ_{ij}) is needed to remove a pair that i in δx would otherwise create with itself. Below we also use the third moment, the density of triplets $Z_{3,ijk}(x, y, z)$, defined in a similar way after removing all non-distinct triplets (Plank and Law, 2015).

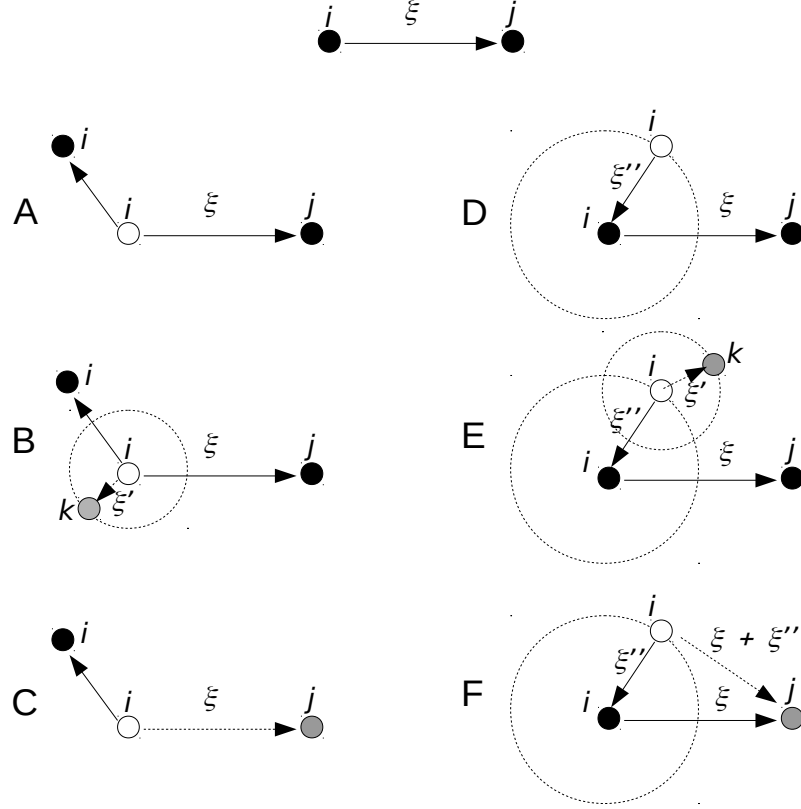


Figure 3: Geometry of the six flux terms A, ..., F in which movement of an individual of type i changes the pair density $Z_{2,ij}(\xi)$ in a model of spatial-moment dynamics, numbered as described in the text. The object at the top is the ij pair: an individual of type j displaced by ξ from the focal individual of type i . Black-filled circles are locations of individuals after movement; empty circles are the positions from which they move; grey circles are neighbours that affect the movement; a dotted circle represents an integration over a neighbourhood; arrows are vectors. Geometries A, B, C in the first column destroy the pair; geometries D, E, F in the second column create the pair. A, ..., F are given as formal expressions (10), ..., (15) in the text.

3.2 Dynamics of the second moment

For simplicity, we consider dynamics in a homogeneous space, meaning that the statistics of the spatial point process in any subdomain are the same, regardless of the location of that subdomain. In this case, the first spatial moment $Z_{1,i}$ is independent of spatial location x . Further, since the model consists only of movement and there is no birth or death, there is no change in first moment over time, so the first moment is simply a constant determined by the fixed population size. The second spatial moment $Z_{2,ij}$ can be expressed as a function of the displacement vector between two individuals $\xi = y - x$, rather than as a function of their physical locations x and y (see Fig. 3 for geometric interpretation). Similarly, the third moment $Z_{3,ijk}$ can be expressed in terms of two displacement vectors, $\xi = y - x$ and $\xi' = z - x$.

Although the first moment is constant, the second moment does change over time as spatial structure develops, as was evident from the pair correlation functions in Fig. 2. The second moment and all higher moments are functions of time, but for clarity we omit the time argument below. The normalised second moment $Z_{2,ij}(\xi)/(Z_{1,i}Z_{1,j})$ relates to the measure of spatial structure in Fig. 2g,h,i; it is the expected value of the pair correlation function $\rho_{ij}(r)$ under isotropy. Thus, to follow the dynamics of the second moment is equivalent to following the behaviour of the average pair correlation function over time. In other words, the dynamics track the development of spatial structure over time. With $Z_{2,ij}(\xi)$ as the state variable, we have a dynamical system describing changes in a function, as opposed to a dynamical system of a scalar quantity, the density of individuals (i.e. we have a partial as opposed to an ordinary differential equation). This is to be expected because the dynamical system has to carry information about the location of individuals relative to one another.

A formal derivation from the stochastic process (Binny et al., 2015, 2016a) leads to six terms affecting the rate of change in the second moment $Z_{2,ij}(\xi)$ due to movement by the focal individual of type i , labelled (A)–(F) below and with geometries illustrated in Fig. 3. Symmetric terms corresponding to movement of the other individual (of type j) in the pair are obtained by making the transformation $\langle i, j, \xi \rightarrow j, i, -\xi \rangle$ to each of the terms below.

First are three negative terms that account for the ways in which an existing pair, consisting of a individual of type i separated from an individual of type j by a vector ξ , can be destroyed. Bias in the movement direction does not enter into these terms, because movement by the focal individual in any direction destroys the pair.

395 (A) Intrinsic rate of movement m_i of the focal individual:

$$396 \quad f_A = -Z_{2,ij}(\xi)m_i. \quad (10)$$

397 (B) Effect of the neighbourhood of the focal individual on its movement
398 rate:

$$399 \quad f_B = -\sum_k \int Z_{3,ijk}(\xi, \xi')w_{ik}(\xi')d\xi'. \quad (11)$$

400 This incorporates the density of neighbours of type k displaced by ξ' from
401 the focal individual (conditional on the presence of the individual of type
402 j displaced by ξ from the focal individual), given by the third moment
403 $Z_{3,ijk}(\xi, \xi')$. The kernel function $w_{ik}(\xi')$ gives a weight to the effect of the
404 neighbour on the movement rate of the focal individual. The overall effect
405 of the neighbourhood is then obtained by integrating over all displacements
406 ξ' and summing over all types k .

407 (C) The other individual (of type j) in the pair also affects the movement
408 rate of the focal individual, with a contribution weighted by $w_{ij}(\xi)$:

$$409 \quad f_C = -Z_{2,ij}(\xi)w_{ij}(\xi). \quad (12)$$

410 Mirroring the negative terms are three positive terms that account for
411 the ways in which a pair, consisting of an individual of type i separated
412 from an individual of type j by a vector ξ , can be created. Since this can
413 only occur via movement, this always starts with an ij pair separated by
414 a different vector, denoted $\xi + \xi''$, followed by a movement by vector ξ'' .
415 These terms are more intricate than those in Eqs. (10)–(12) because they
416 have to cover all possible starting locations for the focal individual and this
417 needs to allow for bias in movement direction.

418 (D) Intrinsic movement rate of the focal individual, allowing for all starting
419 points:

$$420 \quad f_D = m_i \int Z_{2,ij}(\xi + \xi'')\mu_{ij}(\xi'', \xi + \xi'')d\xi''. \quad (13)$$

421 Here, the term inside the integral is the probability of starting with an
422 ij pair separated by vector $\xi + \xi''$, followed by a movement by ξ'' of the
423 individual of type i , which happens with probability density $\mu_{ij}(\xi'', \xi + \xi'')$
424 (see below). This is then integrated over ξ'' to allow for all possible starting
425 locations.

426 (E) Effect of the neighbourhood of the focal individual on its movement
427 rate, depending on its starting location:

$$428 \quad f_E = \int \mu_{ij}(\xi'', \xi + \xi'') \left(\sum_k \int Z_{3,ijk}(\xi + \xi'', \xi')w_{ik}(\xi')d\xi' \right) d\xi''. \quad (14)$$

429 This is similar in structure to (11), accounting for the influence on the focal
430 individual's movement rate of a third individual of type k at displacement

431 ξ'' . The outer integral over ξ'' allows for all possible starting locations for
 432 the focal individual.

433 (F) The other individual (of type j) in the pair also affects the movement
 434 rate of the focal individual:

$$435 \quad f_F = \int Z_{2,ij}(\xi + \xi'') \mu_{ij}(\xi'', \xi + \xi'') w_{ij}(\xi + \xi'') d\xi''. \quad (15)$$

436 This is similar in structure to (13), but instead of the intrinsic movement
 437 rate m_i , accounts for the contribution to the focal individual's movement
 438 rate from the other individual (of type j) in the pair. When the pair is
 439 initially separated by vector $\xi + \xi''$, this contribution is $w_{ij}(\xi + \xi'')$. Again,
 440 the integral over ξ'' allows for all possible starting locations.

441 The key ecological information for movement bias is contained in $\mu_{ij}(\xi'', \xi +$
 442 $\xi'')$, which is the probability density that the focal individual's movement
 443 vector is ξ'' , conditional on the presence of an individual of type j located at
 444 $\xi + \xi''$ relative to the focal individual. This is the movement vector needed
 445 to create the ij pair separated by ξ as required. As with the stochastic
 446 model (Eq. (2)), this is composed of two independent parts:

$$447 \quad \mu_{ij}(\xi'', \xi + \xi'') = f_i(|\xi''|) g(\arg(\xi''), \eta_{ij}(\xi + \xi'')). \quad (16)$$

448 The first part $f_i(|\xi''|)$ relates to the distance moved by an individual of
 449 type i , which is independent of the neighbourhood and given by Eq. (3).
 450 The second part $g(\arg(\xi''), \eta_{ij}(\xi + \xi''))$ is the probability density of mov-
 451 ing in direction $\arg(\xi'')$, which does depend on the neighbourhood. This
 452 dependence is encapsulated in the expected bias vector $\eta_{ij}(\xi + \xi'')$ for an
 453 individual of type i separated from an individual of type j by a vector
 454 $\xi + \xi''$:

$$455 \quad \eta_{ij}(\xi + \xi'') = \beta_i \left(\sum_k \int \nabla v_{ik}(\xi') \frac{Z_{3,ijk}(\xi + \xi'', \xi')}{Z_{2,ij}(\xi + \xi'')} d\xi' + \nabla v_{ij}(\xi + \xi'') \right) \quad (17)$$

456 Here $\nabla v_{ik}(\xi')$ is the gradient vector of the bias kernel $v_{ik}(\xi')$. Eq. (17)
 457 integrates over the neighbourhood of the focal individual for neighbouring
 458 individuals of type k , then sums over all types k , and adds the effect of
 459 the partner individual of type j in the pair. The parameter β_i gives an
 460 overall weight for the bias. The bias vector provides the parameters for a
 461 circular probability distribution. To match the stochastic model, we use a
 462 von Mises distribution with peak angle $\arg(\eta_{ij})$ and concentration $|\eta_{ij}|$, to
 463 obtain the probability density function of the angle $\arg(\xi'')$.

464 Summing expressions (10)–(15), gives the total rate of change of the pair
 465 density $Z_{2,ij}(\xi)$:

$$466 \quad \frac{\partial}{\partial t} Z_{2,ij}(\xi, t) = f_A(\xi, t) + \cdots + f_F(\xi, t) + \langle i, j, \xi \rightarrow j, i, -\xi \rangle, \quad (18)$$

where the matching symmetric terms for the partner individual in the ij pair are given by the substitutions $\langle i, j, \xi \rightarrow j, i, -\xi \rangle$ (Plank and Law, 2015). We give the function arguments in full to make clear the time dependence. This is a formal, exact description of how the movement rules at the level of the individual translate into a dynamical system of pair densities at the macroscopic level, after averaging over many realizations of the stochastic process, starting from the same statistical distribution.

3.3 Closure of the second-moment dynamics

The dynamical system is not yet closed, because it contains the third spatial moment, the density of triplets. To deal with this, a closure approximation is needed to replace the third moment by a function of lower-order moments. Although not usually recognized, closures are ubiquitous in ecological theory: ignoring spatial structure completely implies a closure of the form $Z_{2,ij}(\xi) = Z_{1,i}Z_{1,j}$, giving a dynamical system for the first moment (average density), i.e. the law of mass action, or the so-called mean-field assumption. A formal theory of closures at second order is a matter for research (Raghib et al., 2011; Dieckmann and Law, 2000; Murrell et al., 2004). Here, we use the Kirkwood closure (Kirkwood, 1935):

$$Z_{3,ijk}(\xi, \xi') = \frac{Z_{2,ij}(\xi)Z_{2,ik}(\xi')Z_{2,jk}(\xi' - \xi)}{Z_{1,i}Z_{1,j}Z_{1,k}} \quad (19)$$

as we have found the exact choice of closure makes little difference when the dynamics deal only with movement (i.e. without birth and death) (see for example Fig 6.3 in Binny (2016)).

3.4 Spatial-moment dynamics as an approximation scheme

After closure, the dynamical system is no more than an approximation for the expected value of the second moment of the stochastic process, because it ignores spatial information carried by higher-order moments. How well does this approximation work? This is analogous to asking how well the mean-field assumption works as a description of population dynamics; the answer to that question is that the approximation is poor if neighbourhoods are important (Raghib et al., 2011). The second-order closure should be better because it does carry spatial information, but would still be expected to become poor as higher-order spatial structure becomes important.

Fig. 4 compares the spatial signal of the spatial-moment dynamics with that of the stochastic individual-based model from which the dynamical

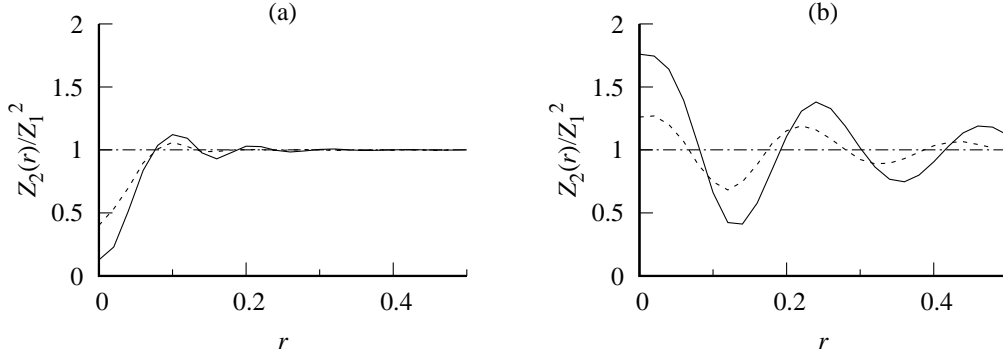


Figure 4: Solutions for the normalised pair density $Z_2(r)/Z_1^2$ of the spatial-moment dynamics, Eqs (18) (19), at time 10 (continuous lines), as a function of the distance r between the pair. These are approximations for the stochastic process of individual movement in Section 2, using parameter values that generated (a) territories in Fig. 2a, and (b) small clusters in Fig. 2b. For comparison, we also show the pair correlation functions (*sensu* Fig. 2g,h) averaged over 100 realizations of the stochastic process at time 10 (dashed lines). Initial conditions were spatial Poisson processes (dash-dot lines). Numerical integration was done by the Euler method, using Eq. (18) (19), discretised as $d\xi = 0.02, dt = 0.05$.

system (18), (19) was derived. For comparability with the stochastic results, we assumed the movement rate to be independent of neighbourhood by setting $w_{ij}(\cdot) = 0$ in Eqs (10)–(15), and leaving in place only an effect of neighbours on the direction of intrinsic movements. This means that the spatial-moment dynamics deal only with terms (10), (13) (geometries A and D in Fig. 3). We examined the dynamics for the bias kernels shown in Fig. 2a,b, as these generate structure at a small spatial scale. We would not expect to find a good approximation with the bias kernel in Fig. 2c, because spatial structure remains at large spatial scales. In other words, the pair correlation $\rho(r)$ does not approach 1 as r increases in Fig. 2i.

Fig. 4 shows that the approximation scheme captures some basic signals of the stochastic, individual-based model. Fig. 4 shows the characteristic regular structure arising from repulsive bias, manifested as a lack of pairs at short distance. Fig. 4 shows the distinct cluster formation as a result of short-range repulsion, medium-range attraction, and long-range repulsion. Although the quantitative match between the stochastic results and the spatial moments approximation is far from perfect, the key qualitative features of the emergent spatial structure are captured in the second moment. This illustrates two key points. First, it shows that the rules responsible for generating the spatial structure in the stochastic model are encapsulated by the dynamical system of spatial moments, despite the latter appearing to be completely different. Second it demonstrates that much of the information about spatial structure is carried just in the second spatial mo-

ment. In other words, there is some justification for closing the hierarchy at second order. The information shown in Fig. 4 would be lost completely in a mean-field model, which implicitly closes the system at the level of the first moment.

4 Discussion

This work draws on recent advances in spatial moment dynamics models of collective cell behaviour (Binny et al., 2016a; Surendran et al., 2018b) to address the issue of animal herding behaviour in ecology, and opens new research avenues in this setting. In particular, we have explored how using different forms of neighbourhood interaction kernels for directionally biased movement can give rise to formation of animal groups or herds. Individual-based models describing biased directional movement have been widely used in an ecological context (Codling and Hill, 2005; Benhamou, 2006; Codling et al., 2007; Bode, 2011). However, this is the first time that a spatial moment dynamics model, capturing the outcomes of this directional bias at the macroscopic scale, has been used to describe animals living in groups. In doing this, we have shown the geometry of six flux terms that describe the exact relationship between the algorithmic individual-based model and the mathematical model (up to the second spatial moment).

Our results show that herd-like spatial structure can be generated solely from interactions among neighbouring individuals of the same species. In reality, this spatial structure can be strongly affected by interspecific interactions, such as the presence of predators. Future work will include explicitly applying the model framework developed here to systems with multiple interacting species. This has been done for cell–obstacle interactions (Surendran et al., 2018b) and chase–escape interactions (Surendran et al., 2018a), but these models use simple attractive or repulsive interactions, rather than the distance-dependent interactions that we employ here.

One advantage of spatial moment approximations over individual-based models is that the equations for the dynamics of spatial moments are deterministic and only need to be solved once, rather than performing computationally intensive repeated simulations. They are also more tractable mathematically, permitting further analysis and exploration of parameter space. Computational power typically restricts simulation of individual-based models to systems with relatively low numbers of individuals, due to the requirements of tracking each individual’s movements and interactions with each of its neighbours over time. There are many such examples of

563 small-herd systems in ecology (see for example Table 1 in Reiczigel et al.
564 (2008)). In contrast, the computational requirement for solving the spatial
565 moments approximation is independent of population size. The methodol-
566 ogy would lend itself to systems with much larger animal herds and offer
567 insights that would otherwise require considerably greater computational
568 resources to achieve through simulations alone.

569 Although the spatial-moment model shows the basic spatial structure,
570 its fit to the stochastic model could clearly be improved. Attenuation of
571 the spatial signal with increasing distance is rather slow in Fig 4b, which
572 generates inaccuracies that can propagate to shorter distances. Also, at the
573 shortest distances, the model overestimates the strength of spatial struc-
574 ture; this may be because, after discretisation, spatial resolution becomes
575 less good as $r \rightarrow 0$. Such issues could be dealt with by discretising over a
576 larger space on a finer spatial grid, but this would have made computation
577 unfeasible. In future work, a Fourier transform for the convolution inte-
578 grals should be considered, as this could provide a major increase in speed
579 of computation.

580 Previous models for animals living in herds have used the idea of zones
581 of attraction and repulsion (Couzin et al., 2002; Bode, 2011). A zone of
582 repulsion is also supported by data (Krause et al., 2002). Zones of repulsion
583 and attraction have also been modelled in the cell behaviour literature,
584 for example using the Lennard-Jones kernel (Jeon et al., 2010) and the
585 Morse potential (Middleton et al., 2014; Matsiaka et al., 2017). Our model
586 incorporates and builds on these ideas, including the possibility for multiple
587 zones of attraction and repulsion with different spatial scales. Examples
588 of the types of behaviour encapsulated by the bias kernels we have studied,
589 and the resulting spatial structure, can be found in real animal populations.
590 For example, Gerum et al. (2018) observed strong regular structure in king
591 penguin (*Aptenodytes patagonicus*) colonies, caused by short-range nest
592 site-protecting repulsive interactions between neighbours. Gajamannage
593 et al. (2017) studied the formation of small clusters in cows (*Bos taurus*),
594 generated by a balancing of costs to an individual of synchronisation (e.g.
595 needing to concede to the timings of a large group, causing interrupted
596 rest or grazing) with the benefits of reduced predation risk for larger, more
597 defensible groups. Olson et al. (2009) observed the formation of a mega-
598 herd in Mongolian gazelles (*Procapra gutturosa*), driven by habitat quality
599 in a fragmented landscape.

600 Some animal behaviour models also have an orientation component to
601 make individuals move in the same direction (Sumpter et al., 2008). This
602 is more relevant for species where individuals in a group tend to be in
603 continuous motion, such as shoaling fish or flocking birds. These situa-

604 tions require a velocity jump process (Codling et al., 2007, 2008), where
 605 reorientation events depend on the distance to and current orientation of
 606 other individuals in the neighbourhood (Agueh et al., 2011). In principle,
 607 the structure of such a population could be described by a second spatial
 608 moment in terms of the difference between the positions and orientations
 609 of two individuals in a pair, but this problem is currently untackled.

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